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PSYCHE

Vol. 68 MARCH, 1961 No. 1

AUSTRALIAN CARABID BEETLES V.[1] TRANSITION OF WET FOREST FAUNAS FROM NEW GUINEA TO TASMANIA

BY P. J. DARLINGTON, JR.
Museum of Comparative Zoology, Cambridge, Mass.

Introduction

Beetles of the family Carabidae (predaceous ground beetles) are numerous in tropical rain forest in New Guinea and numerous also (but less diverse) in cool south temperate rain forest in Tasmania, but no species and hardly any genus is common to the two faunas, and even the dominant tribes are different. However there is no single boundary between the New Guinean and Tasmanian faunas, but a broad and complex transition, which I shall try to describe.

My interest in this part of the world began with the Harvard Australian Expedition of 1931-1932, when I collected Carabidae in eastern Australia north to part of the Cape York Peninsula, as well as in southwestern Australia. In 1943-1944 I spent eleven months in New Guinea as an army entomologist, and was able to collect Carabidae especially in lowland rain forest at Dobodura, Papua, while hospitalized there, and in mountain forest on the Bismarck Range, Northeast New Guinea, in lieu of leave. I have sorted and arranged my own and much borrowed material and am now more than half way through writing "The Carabid Beetles of New Guinea" (see Darlington 1952), so that I have a good knowledge of New Guinean Carabidae. Recently, from December 1956 to June 1958, I have been again in eastern Australia, traveling and living in a small truck with my wife and fourteen-year-old son, and collecting Carabidae in practically every important piece of wet forest from the northern tip of Cape

[1]Earlier parts of this series are listed in the reference list at the end of this paper.

York to the southern tip of Tasmania.[2] A brief itinerary with maps and list of localities has been published (1961). Information and collections obtained during this trip have enabled me to correlate other information and write the present paper. New genera and species referred to now (but not by name) will be described in forthcoming numbers of *Psyche* and *Breviora.*

The Forests

My "wet forests" are rain forests as classified in "The Australian Environment" (CSIRO 1950, 77-96). That is, they are dense, evergreen (non-deciduous) forests with closed canopies, often (in tropical rain forest) with many woody vines, but with comparatively little low vegetation, the ground being covered with dead leaves and leaf mold rather than grass or herbs.

Two main types of rain forest exist in the Australian Region: tropical (including subtropical) (Figs. 1, 2) and south temperate (Figs. 3, 4). Tropical rain forest is widely distributed in New Guinea at low and middle altitudes, although in the drier country of southern New Guinea it is replaced by op n savannah woodland like that of much of northern Australia. Tropical rain forest occurs also on the eastern edge of Australia in separate tracts spaced irregularly from parts of Cape York south through Queensland and northern New South Wales (map, Fig. 6). The best of this forest in tropical and subtropical Australia as well as in New Guinea is real, Malaysian-type rain forest, although some tracts in Australia are lighter and seasonally drier, and light rain forest sometimes grades into semi-deciduous monsoon forest.

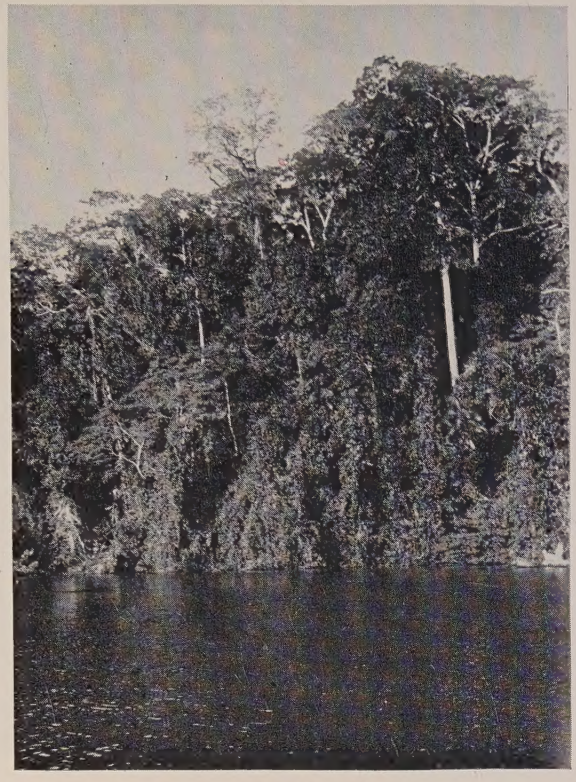
The northernmost rain forest in Australia is the tip-of-peninsular (Lockerbie or Somerset) tract on the tip of Cape York. It is lowland rain forest, but somewhat depauperate (see p. 17).

[2]This trip was supported in part by a fellowship of the John Simon Guggenheim Memorial Foundation. I am especially indebted to Dr. L. J. Webb, of the Commonwealth Scientific and Industrial Research Organization, for information on the distribution of rain forest in Queensland, to many members of the Queensland Department of Forestry who aided or guided us in the field, and to Mr. P. J. Killoran, of the Queensland Department of Native Affairs, who arranged our visit to Bamaga and the tip of Cape York. I very much regret that I do not have space to acknowledge other assistance in detail here.

EXPLANATION OF PLATE 1

Fig. 1. Tropical rain forest, Lake Barrine, Atherton Tableland, North Queensland (P. J. D. 1932).

Fig. 2. Interior of tip-of-peninsular (tropical) rain forest, from edge of new clearing, Lockerbie, Cape York, Queensland (P. J. D. 1958). This is the habitat of *Mecynognathus.*



1

2

3

4

Next in order southward is a gap more than 100 miles wide of drier, open savannah woodland (Fig. 5) in which may be an isolated piece of rain forest near the head of the Jardine River, unknown biologically (Brass 1953, pp. 154, 161).

Next is the mid-peninsular rain forest system. It extends irregularly and with perhaps slight interruptions from near Iron Range and Mt. Tozer south to the "Rocky Scrub" east of Coen. Altitudinally it extends from near sea level (*e.g.* at Iron Range) to about 2,000 ft. on the higher summits of the McIlwraith Range. It includes fairly heavy rain forest, although its quality varies locally.

Fig. 5. Rather dry savannah woodland northeast of Coen, Cape York peninsula. (P. J. D. 1932). Such woodland is an effective barrier to rain forest Carabidae in the tropics.

Next, after another gap more than 150 miles wide of drier, open woodland, is the base-of-peninsular or main tropical rain forest system of North Queensland. Outlying pieces of semi-rain forest of this system are within sight of Cooktown, and heavier rain forest begins on the coastal mountains (Mt. Amos, Mt. Finnigan) about 20 miles to

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EXPLANATION OF PLATE 2

Fig. 3. South temperate rain forest, Lake St. Clair, Tasmania (P. J. D. 1957). On left is transitional wet forest with overstory of big eucalypts; center, heavy rain forest including *Nothofagus*.

Fig. 4. Interior of old south temperate rain forest, Cradle Valley, northern Tasmania (courtesy Mr. H. J. King, Honorary Photographer, and Mr. Frank Ellis, Director, Queen Victoria Museum, Launceston).

the south. From here an irregular system of good rain forests extends somewhat discontinuously but with no very wide breaks south to and across the Atherton Tableland and farther south along a series of plateaus and ranges to the Mt. Spec plateau (Paluma Range) almost within sight of Townsville. Much of this forest system lies between 1,000 and 5,000 ft. altitude, but areas of good rain forest belonging to it occur (or occurred before being cleared) also on the coastal plain east of the Atherton Tableland and in the Mossman-Daintree region.

From the southern end of the main tropical rain forest system to below Rockhampton is a gap of nearly 500 miles of dry, open woodland broken only (so far as I know) by two noteworthy islands of rain forest. One is at about 3,000-4,000 ft. on the crest of the Elliot Range, within sight of (southeast of) Townsville but separated from the northern rain forests by a low, comparatively dry valley. The other, more important island of rain forest is on the Eungella Range about 40 miles inland from Mackay, at about 2,000-4,000 ft. altitude. Scattered fragments of semi-rain forest, for example near Proserpine (Repulse Bay) and Yepoon (Byfield), are relatively unimportant so far as carabid distribution is concerned.

South of Rockhampton, in the edge of the south temperate zone, begins what I call the subtropical rain forest system. The first piece of (rather poor) rain forest of this system is on Mt. Jacob east of Many Peaks. Other tracts are widely scattered in southeastern Queensland at low altitudes as well as on mountains (Blackall Range, Bunya Mts., Mt. Tamborine, McPherson Range on the New South Wales border, etc.). The different forest tracts vary in quality, but the best of them approximate tropical rain forest. This system of rain forests extends into northeastern New South Wales at rather low altitudes, although much of it has now been cleared. The more important pieces that still remain are listed and briefly described in my published locality list (1961). The most southern *good* tract that seemed to me to be tropical-type rain forest is on "Mt. Dorrigo", on the lower (eastern) edge of the Dorrigo Plateau, at about 30° 20′ S., but small pockets of more or less similar forest occur still farther south, even south of Sydney, especially in wet ravines.

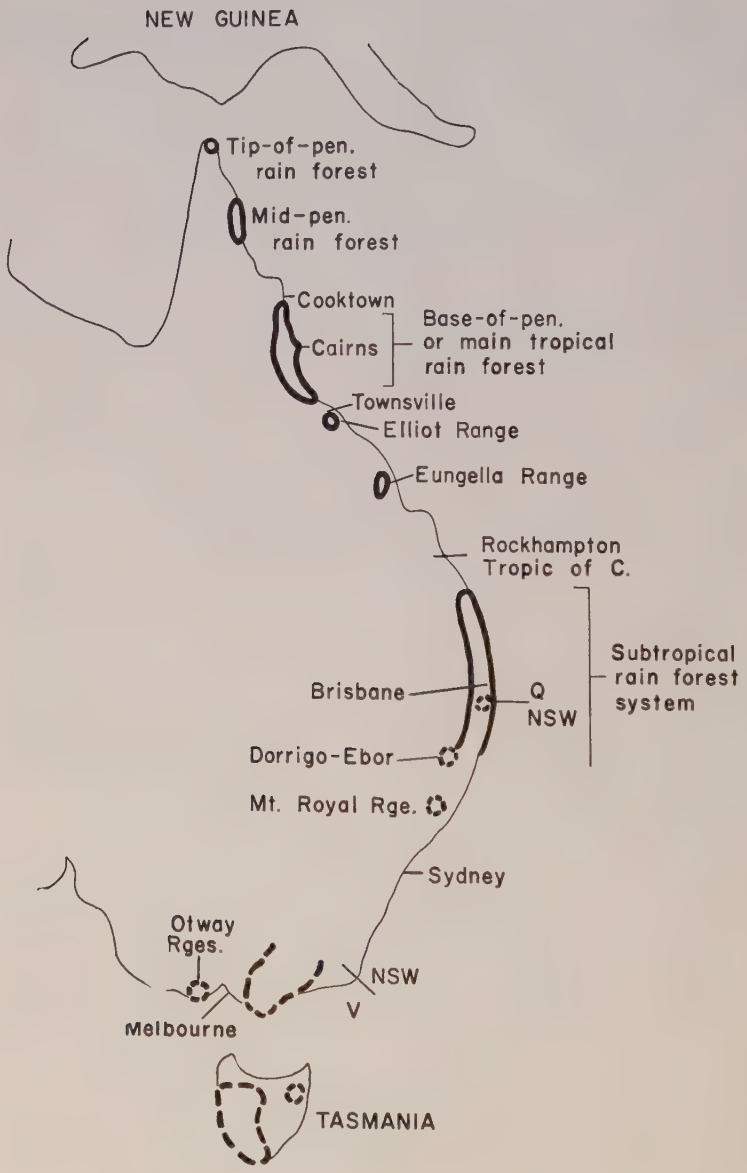
South temperate rain forest (see again Figs. 3, 4) is different in aspect from tropical rain forest (fewer vines, etc.) and different botanically, often dominated by southern beeches (*Nothofagus*). Such forest is widespread in southwestern Tasmania and occurs in isolated tracts elsewhere in Tasmania (see paper referred to above for details). Isolated tracts of similar forest occur on plateaus and mountains in southern Victoria including the Otway Ranges southwest of

Melbourne and some of the southern "Victorian Alps" east of Melbourne. This kind of forest occurs also, at wide intervals, on isolated plateaus in eastern New South Wales, notably on the plateau of the Mt. Royal Range (Barrington Tops and Tomalla Tops) at about 31° 50′ S. and on the higher part of the Dorrigo-Ebor Plateau (especially at Point Lookout in New England National Park) at about 30° S. Both these plateaus reach about 5000 ft. above sea level. The northernmost *Nothofagus* in Australia is still farther north, on the southern border of Queensland, where small tracts of old trees exist on the highest points of the McPherson Range, at about 28° 20′ S. and 4,000 ft. altitude. *Nothofagus* does not occur on the mountains of tropical North Queensland but is dominant in New Guinea in mountain forests between about 6,500 and 10,000 ft. (Womersley and McAdam 1957, p. 25). However, south temperate groups of Carabidae do *not* occur in the New Guinean *Nothofagus* forests.

The distribution of tropical (including subtropical) and south temperate rain forest is shown, rather diagramatically, on the accompanying map (Fig. 6). The map is based partly on the vegetation map in "The Australian Environment" (CSIRO 1950, pp. 88-89) and on Brass's (1953, p. 152) map of Cape York rain forests, but many details are modified according to my own observations. In most cases rain forest is not continuous within the boundaries shown, but occurs as irregular, sometimes discontinuous tracts and strips interspersed with savannah woodland (in the north) and/or sclerophyll forest (in the south). The two kinds of rain forest overlap widely in New South Wales. Within the area of overlap south temperate rain forest is usually above (at higher altitude than) tropical rain forest, but there is some mixing.

The Carabidae

The wet-forest Carabidae of New Guinea and Australia, including Tasmania, are numerous, diverse, and complex in ecology and distribution. They form three general ecological groups. Those that live on the ground without being specially associated with surface water are mesophiles or *geophiles*. Those that live on the ground beside streams or ponds or in swamps are *hydrophiles*. And those that live on tree trunks or in foliage above the ground are *arboreal*. According to my (1943, p. 41) rough analysis of the Australian carabid fauna, at least half the species are geophiles, not quite a quarter hydrophiles, and not quite a quarter arboreal. The carabid fauna of New Guinea divides in something like the same way, although I cannot yet give exact figures.


NEW GUINEA
Tip-of-pen. rain forest
Mid-pen. rain forest
Cooktown
Cairns
Base-of-pen. or main tropical rain forest
Townsville
Elliot Range
Eungella Range
Rockhampton
Tropic of C.
Subtropical rain forest system
Brisbane
Q
NSW
Dorrigo-Ebor
Mt. Royal Rge.
Sydney
Otway Rges.
NSW
V
Melbourne
TASMANIA

State of wings of Carabidae is correlated with ecology and distribution. Most Carabidae in most parts of the world have fully developed inner wings and can fly, but some have lost their wings (except for vestiges) and become flightless. The Australian carabid fauna includes an unusually large proportion of flightless species: according to my rough analysis (*loc. cit.*), nearly 45% of all Australian Carabidae have atrophied wings, and many genera and even some tribes are wholly flightless. Most hydrophiles and arboreal forms have retained their wings and can fly, but about 75% of Australian geophile Carabidae are flightless, and flightless groups are common everywhere in Australia, at low and high altitudes and in wet and dry climates, and some are well represented in the tropical as well as the temperate parts of the continent. In New Guinea flightnessess is rare among lowland Carabidae. This accords with the general rule that most Carabidae in most wholly tropical lowland areas are winged. On mountains in New Guinea, however, as on many tropical mountains elsewhere, flightless geophile Carabidae are numerous.

New Guinea-Tropical Australian Relationships

Probably the first fact that strikes entomologists collecting in the rain forests of tropical Australia is that some of the insects are species that occur in New Guinea. This is expected. The Australian rain forests themselves are predominantly New Guinean (or Malaysian) both in aspect and in botanical relationships (CSIRO 1950, pp. 95-96; Brass 1953, p. 154); many mammals in the North Queensland rain forests belong to New Guinean genera or even species; and so do many birds. Some Carabidae are common to New Guinean and Australian rain forests. For example *Syleter papua* Darl. extends to the tip of Cape York, living on the ground in shaded swamps. *Morion longipenne* Putz. of New Guinea extends to the main North Queensland rain forests, on and in fallen logs. And *Violagonum violaceum* (Chd.) is common in rain forest in New Guinea and eastern Australia south at least to near Rockhampton, in accumulations of dead leaves on the ground and in thick foliage. Besides shared species like these (there are many others among Carabidae) the New Guinean and Australian rain forests share some geographically restricted genera, for example *Platycoelus (Chlaenioidius)*, *Loxandrus*, and *Stricklandia*,

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Explanation of Plate 3

Fig. 6. Distribution of rain forests in eastern Australia. Solid lines enclose principal areas of tropical (including subtropical) rain forest; broken lines, of south temperate rain forest. In most cases rain forest is not continuous within the boundaries shown but occurs in discontinuous or scattered tracts. See text for further details.

as well as many more-widely distributed genera. Up to a point, therefore, the Carabidae agree with the forest trees, mammals, and birds in showing a considerable number of species and genera common to the rain forests of New Guinea and tropical Australia.

When I was collecting on the Atherton Tableland in northeastern Australia in 1932, I found not only many Carabidae of obviously New Guinean groups but also, in rain forest, many species of Australian groups not known to occur in New Guinea. Included were striking endemic species of *Notonomus, Trichosternus, Leiradira, Pamborus,* and *Mystropomus.* Knowing, as I did, that the rain forests of Australia and New Guinea had much in common, and knowing that the Carabidae of New Guinea were poorly collected, I imagined in New Guinea a rich fauna of the genera just named, perhaps in rain forest at middle altitudes, but wholly unknown. It was a sort of El Dorado for the future, to a young and enthusiastic carabid student. But now that I have collected in New Guinea and seen thousands of Carabidae collected there by other persons, I know that this El Dorado does not exist, and I know why. All the Carabidae common to the New Guinean and Australian rain forests are winged and probably fly. All the genera mentioned above as represented in rain forest on the Atherton Tableland are wholly flightless, and I know now that there is no direct relationship between any flightless Carabidae of the New Guinean and Australian rain forests.[3]

The difference between the flightless Carabidae of Australia and New Guinea goes far beyond mere differences of species and genera. The composition and origins of the two faunas are fundamentally different. Flightless Carabidae are numerous everywhere in Australia, even at low altitudes in the tropical part of the continent including Cape York. Many of the species belong to wholly flightless genera or even flightless tribes that have evidently been in Australia a long time. Derivatives of old Australian flightless groups dominate the flightless ground-living carabid fauna of tropical rain forest in Australia. In New Guinea, in contrast, no primarily flightless groups of Carabidae occur at low altitudes. A very few species of the primarily winged

[3]If tiger beetles are considered Carabidae, *Tricondyla aptera* Ol. is an exception to this rule. The genus *Tricondyla* is primarily Oriental and is wholly flightless. Nevertheless *T. aptera* has reached New Guinea, probably rather recently (it is only slightly differentiated there), and has got beyond New Guinea to the mid-peninsular rain forests of Cape York. (It has reached the Solomon Islands and New Hebrides too.) It is a good sized (nearly an inch long), big-eyed, ant-like, active insect, which lives on tree trunks in rain forest. It has probably dispersed on floating trees, which ground-living Carabidae are not likely to do.

genera *Clivina, Tachys, Lesticus, Platycoelus,* and *Loxandrus* have undergone wing atrophy at low altitudes in New Guinea (Darlington in press), but they have evidently done it recently, *in situ*. Some of the species are still dimorphic, with fully winged individuals occurring with the short winged ones, and all the short winged lowland species are closely related to long winged ones that still exist in New Guinea. It is only above about 5000 ft. in the mountains that flightless Carabidae become numerous in New Guinea, and they too have apparently undergone wing atrophy *in situ*. That is, they have been derived on the mountains of New Guinea from winged ancestors, and do not represent flightless stocks of other regions. This is my conclusion after making formal studies of the New Guinean representatives of the two principal tribes concerned, the Agonini (Darlington 1952, especially table p. 108) and Pterostichini (in press).

Besides the change of specific flightless stocks from New Guinea to Australia there is a change of dominance of tribes. In New Guinea, Agonini are much more numerous than Pterostichini, and most flightless Carabidae of the island are agonines. But in Australia, even in the tropical rain forest, Pterostichini are overwhelmingly dominant and include most of the flightless forms. This striking shift of dominance is further discussed on page 22.

The first important finding of the present study, then, is that, although the rain forests of New Guinea and tropical Australia are similar and share many species of plants, mammals, birds, and winged insects including many winged Carabidae, they have wholly different faunas of flightless Carabidae, which differ not only in taxonomic details but also in general ecology (in relation to altitude), in origin of the flightless stocks, and in relative dominance of tribes.

Transition in Australia: South from the Tropics

Now to be considered is the transition of wet forest carabid faunas within the limits of Australia and Tasmania.

Five important genera of flightless geophile Carabidae are mentioned above as occurring in rain forest on the Atherton Tableland. Of these five genera, *Notonomus* is most dominant. It is a genus of about 100 species, confined to eastern and southeastern Australia and Tasmania except for one species isolated in southwestern Australia. The genus' northern limit is between Daintree and Cooktown. It is represented by several species (some very localized) in the main tropical rain forest system of North Queensland, where it seems to be confined to rain forest. It is well represented in the subtropical rain forests of South Queensland and northern New South Wales and south through

eastern New South Wales and southern Victoria; in these areas some species occur not only in rain forest (including south temperate rain forest) but also in wet sclerophyll forest and good savannah woodland. However only two groups of the genus reach Tasmania and only one group (two related, primarily allopatric species) occurs in rain forest there.

Trichosternus is a genus of 25 or more species confined to eastern Australia, except that one species is isolated in southwestern Australia (Darlington 1953, p. 94). The genus' northern limit is between Daintree and Cooktown. It occurs (several species, some very localized) throughout the main rain forest system of North Queensland, where it is apparently confined to rain forest. It is well represented also in the subtropical rain forest system of South Queensland and northern New South Wales, and in this area some species occur in savannah woodland as well as in tropical-type rain forest, and some have entered south temperate rain forest on the Dorrigo-Ebor plateau and the Mt. Royal Range. The southern limit of the genus is somewhere in east-central New South Wales, probably not far north of Sydney.

The northern limit of *Leiradira* (or of the group of genera that includes *Leiradira*) is between Daintree and Cooktown. This genus too occurs in much of the main tropical rain forest system of North Queensland, being represented there by several distinct species each more or less localized, but the genus may be absent in the southern extension of the main tropical rain forest system south of the Atherton Tableland. It is represented also by several species in the subtropical rain forests of South Queensland etc. Its southern limit is apparently on the lower, eastern edge of the Dorrigo plateau. It is confined to eastern Australia. It is wholly or chiefly a rain forest genus in all parts of its range.

The three preceding genera are all Pterostichini. All their species are flightless geophiles. Additional flightless geophile pterostichines are localized in all the different rain forest areas of Australia from Cape York to Tasmania. Examples are *Mecynognathus* in the tip-of-peninsular forests; *Paranurus* in the mid-peninsular forests; *Loxogenius* and undescribed genera in the main tropical rain forest system; *Nursus s. s., Liopasa, Ceratoferonia, Zeodera,* and *Notolestes* in the subtropical rain forest system; *Loxodactylus* in the wet forests of southern Victoria; and *Rhabdotus* in those of Tasmania. (It should be added that Australia possesses many winged pterostichines as well as these and other flightless genera.)

Of non-pterostichines, *Pamborus* is noteworthy. It is confined to eastern Australia and is one of the two known genera of the tribe Pamborini. (The other is monotypic *Maoripamborus* in New Zealand — Brookes 1944.) The northern limit of *Pamborus* is probably near Cooktown. Four species of the genus occur in the main tropical rain forest system of North Queensland, chiefly or wholly in rain forest. Six other species occur in South Queensland and New South Wales. Some of them occur mainly in (sub)tropical rain forest, but *viridis* inhabits savannah woodland and some other species occur in open woods as well as rain forest, and some enter south temperate rain forest on the high plateaus of north-central New South Wales. The southern limit of the genus is near the Shoalhaven River about 70 miles south of Sydney. (Old records for Victoria are probably errors.)

The genus *Mystropomus* is the only Australian representative of the pantropical tribe Ozaenini. The genus is confined to eastern Australia. Its northern limit is between Daintree and Cooktown. A single species (two subspecies) occurs throughout the main tropical rain forest system of North Queensland, and is apparently confined to rain forest. Another, variable species (two subspecies) occurs in the subtropical rain forest system, and extends into more open woodland. The southern limit of the genus is apparently near Sydney.

These five genera dominate the flightless geophile carabid faunas of the main tropical and subtropical rain forest systems of eastern Australia. Their distribution is notable in several ways. All five genera reach an approximately common northern limit, north of Daintree and south of or near Cooktown. All five genera are widely distributed both in the main tropical and in the subtropical rain forest systems. These two forest systems are separated by a wide barrier of comparatively dry, open forest in which is one important "island" of rain forest, on the Eungella Range west of Mackay, and all five of the genera in question are represented there.[4] In the tropics, these genera occur only or chiefly in rain forest,[5] although most of them enter opener forest too in the south temperate zone.

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[4]Of the 5 genera in question on the Eungella Range, the one *Pamborus* has close relatives in both North and South Queensland. The one *Mystropomus* is a South Queensland species. Of 2 *Trichosternus*, one probably belongs to a South Queensland group and the other is doubtful. The one *Notonomus* belongs to a North Queensland group. And the one *Leiradira* belongs to a South Queensland subgenus. These genera in the Eungella rain forest therefore show 2 close ties with North Queensland (in *Pamborus* and *Notonomus*) and 4 with South Queensland.

[5]*Trichosternus cordatus* Chd. occurs outside rain forest in the southern edge of the tropics.

Southward, through New South Wales, rain forest of (sub)tropical type diminishes in area and quality, and the Carabidae associated with it diminish too. Of the five genera just discussed, *Leiradira* may not extend south of the Dorrigo. *Trichosternus, Mystropomus,* and *Pamborus* go a little farther south, reaching different limits probably in this order, but do not reach Victoria. And *Notonomus* reaches Victoria (in numbers) and Tasmania (only one stock in rain forest). Toward their southern limits, all these genera, except *Leiradira,* occur not only in tropical-type rain forest but also in opener forest, and all, except again *Leiradira,* have entered or even evolved endemic species in south temperate rain forest on the Dorrigo-Ebor plateau and the Mt. Royal Range.

Transition in Australia: North from Tasmania

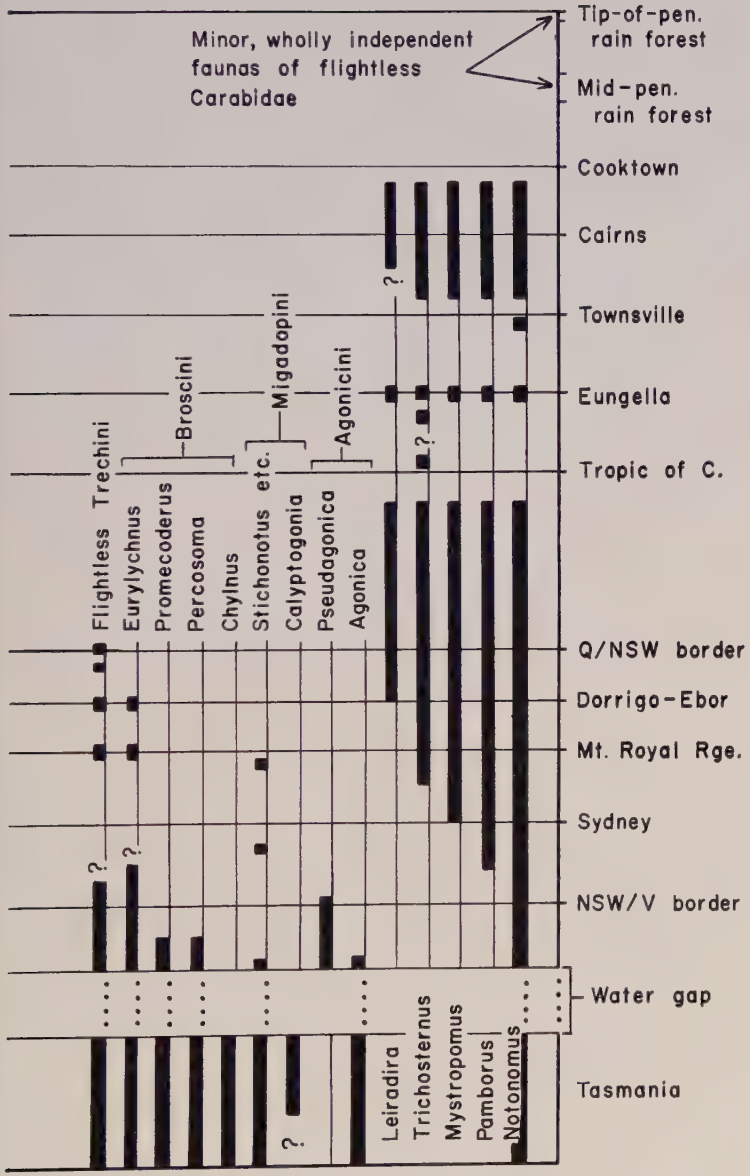
The ground-living Carabidae of the south temperate rain forest of Tasmania are dominated by or include flightless genera of four special tribes in addition to the more widely distributed Pterostichini, Licinini, etc.

The tribe Broscini is well represented in both the north and the south temperate zones of the world (Ball 1956) but is absent in the tropics or nearly so. Some northern broscines have well developed wings, but I think that all those of the southern hemisphere have atrophied wings and are flightless. Four genera occur in Tasmania. *Promecoderus* is represented there by several rain forest species and by other species that live in drier, opener woodland. The genus is widely distributed across southern Australia, but chiefly in dry forest and arid country, although one or two species occur in rain forest in Victoria. Of the other Tasmanian genera, *Chylnus* is confined to Tasmania, in wet forest. *Percosoma* occurs in Tasmania and the mountains of southeastern Victoria, in wet forest. And *Eurylychnus* occurs in Tasmania, southern Victoria etc. including the Otway Ranges, and east and north into southern New South Wales, and two separate stocks of the genus have species isolated (chiefly in south temperate rain forest) on the Mt. Royal Range and the Dorrigo-Ebor plateau. The latter is the northern limit of wet-forest broscines in Australia.

The tribe Trechini (subfamily Trechinae of Jeannel 1926-1928)

Explanation of Plate 4

Fig. 7. Diagram of transition of selected flightless geophile Carabidae in rain forests of eastern Australia. The 5 genera at bottom of the diagram are primarily tropical and subtropical; the other genera and tribes, primarily south temperate. See text for further details.


Minor, wholly independent faunas of flightless Carabidae
Tip-of-pen. rain forest
Mid-pen. rain forest
Cooktown
Cairns
Townsville
Eungella
Tropic of C.
Q/NSW border
Dorrigo-Ebor
Mt. Royal Rge.
Sydney
NSW/V border
Water gap
Tasmania
Flightless Trechini
Eurylychnus
Promecoderus
Percosoma
Chylnus
Stichonotus etc.
Calyptogonia
Pseudagonica
Agonica
Broscini
Migadopini
Agonicini
Leiradira
Trichosternus
Mystropomus
Pamborus
Notonomus

is world-wide in distribution. It includes both flying and flightless genera, but the flying genera usually live beside standing or running water and are not forest-living geophiles. Flightless geophile Trechini are numerous both north and south of the tropics. In Tasmania they are numerous in south temperate rain forest and hardly enter other habitats at low altitudes, although some occur in open country above timber line, on cold mountain tops. Flightless Trechini are less numerous but still widely scattered in wet forests and on mountain tops in southern Victoria, including the Otway Ranges (Moore 1960), east nearly to the New South Wales border and north to Mt. Kosciusko in southern New South Wales, and endemic species perhaps representing one original flightless stock of spotted *"Trechus"* are isolated on the Mount Royal Range, the Dorrigo-Ebor plateau, and the McPherson Range on the Queensland border.[6]

The tribe Migadopini (Jeannel 1938; Darlington 1960, p. 663) is confined to the southern hemisphere, with different genera localized in Tasmania and southeastern Australia, New Zealand, and the southern tip of South America, etc. Two flightless genera of the tribe occur in Tasmanian rain forest: *Calyptogonia* is confined to Tasmania; *Stichonotus* extends to the mainland, but only to the Otway Ranges. A third Australian genus of the tribe is known from a single specimen collected long ago near Kiama south of Sydney, and a fourth genus occurs still farther north, in subtropical forest on the low (*c.* 2,000 ft.) Comboyne plateau at about 31° 35′ S. This last genus, *Decogmus*, differs from all other Migadopini in being winged.

Finally, the flightless tribe Agonicini is confined to Tasmania and southeastern Australia (Moore 1960). There are two genera. One is widely distributed in Tasmania and occurs also in the mountains of southern Victoria east of Melbourne (B. P. Moore, in letter). The other is confined to the mainland, including the Otway Ranges and the "Victorian Alps," north to Mt. Kosciusko. Agonicines live on the ground in rain forest, and sometimes in open snow gum woods on mountains.

Although there are other Carabidae in Tasmanian rain forests (especially various Pterostichini and Licinini) the four tribes just discussed make up a large part, and zoogeographically the most important part, of the flightless wet forest Tasmanian carabid fauna. It will be seen from details given above that all four tribes occur both in

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[6]A second *"Trechus", diemensis* Bates, extends from Tasmania and southeastern Australia north to the McPherson Range, but this species is winged or dimorphic.

Tasmania and on the adjacent mainland of Australia, but that they all diminish rapidly northward.

The transition of selected elements of the flightless geophile carabid faunas of tropical and south temperate rain forests is diagrammed in Fig. 7.

Isolated Australian Faunules

To return to the five carabid genera discussed above as characteristic of the main tropical and subtropical rain forests, these genera have distributions that are alike in many details. Within the main (base-of-peninsular) tropical rain forest system, they all have almost the same northern limits and (excepting perhaps *Leiradira*) the same southern limits. All are represented on the Eungella Range. In South Queensland, all apparently find their northern limit on Mt. Jacob (except that *Trichosternus cordatus* extends farther north in drier woodland), and all extend well into New South Wales, although they reach different limits there. They illustrate a general fact, that the carabid faunas of the main tropical and subtropical rain forest systems of eastern Australia, although separated by several hundred miles of comparatively dry country, are fundamentally similar, dominated by the same tribes, and share many genera some of which coincide remarkably in details of distribution, although some other genera and most species are different. However three isolated pieces of Australian rain forest have carabid faunules that do not fit into this main pattern. They are the tip-of-peninsular and mid-peninsular rain forests of Cape York and the rain forest on the Elliot Range south of Townsville.

The tip-of-peninsular tract is light rain forest and is limited both botanically and zoologically. For example, stinging trees *(Laportea)*, which occur in other Australian rain forests and in New Guinea, are apparently absent in the tip-of-peninsular forest, and land leeches and itch mites, which are pests in rain forest elsewhere, are apparently absent in the tip-of-peninsular tract. The winged Carabidae of this tract are not remarkable, except that they include New Guinean species. But the flightless Carabidae form a faunule wholly different from that of any other rain forest, consisting (so far as I could find) of only two flightless species. One is *Mecynognathus dameli* Macl., an enormous carabid, the largest males 2½ inches long with mandibles like stag beetles. The genus occurs nowhere else on earth, although it may be rather closely related to *Paranurus* (see below). The other is a large flightless *Clivina* (probably *kershawi* Sl.), which is fairly common both in the rain forest and in adjacent savannah woodland. The nature of this forest and of its flightless Carabidae suggests that

the tip-of-peninsular tract is not a remnant of a larger, continuous rain forest but has been constituted or reconstituted separately, by gradual accumulation of a limited variety of plants and animals.

The mid-peninsular rain forests of Cape York are heavier and more extensive than the tip-of-peninsular tract, more like the base-of-peninsular forests at least superficially, but their flightless Carabidae form a second independent faunule. None of the flightless genera characteristic of the other rain forests is represented in the mid-peninsular system. In their place is a single large species of *Paranurus*. This is a genus of probably only one, geographically variable species, which occurs from the tip of Cape York (and islands off the tip) south to below Cairns mainly in good savannah woodland. In most parts of its range it apparently does not enter rain forest, but it has done so in the mid-peninsular system, where it is now widely distributed. It seems to have invaded this system recently. An earlier invasion of the tip-of-peninsular rain forest by the ancestral stock of *Paranurus* may have produced *Mecynognathus*. There is also in the mid-peninsular rain forest a flightless *Coptocarpus,* but it is small and rare and I am not sure of its habitat or relationships. And also in this forest is a large form of *Lesticus chloronotus* Chd. It is winged, but its distribution and behavior suggest that it may eventually become flightless, as several stocks of the same genus have done in New Guinea. The Carabidae, then, suggest that the mid-peninsular rain forest has not been connected with the main base-of-peninsular system but, like the tip-of-peninsular tract, has derived or is deriving its flightless Carabidae independently.

The rain forest on the Elliot Range is poorly known. The only insect collecting ever done in it, so far as I know, was done March 2, 1958, when my son and I climbed from Double Creek to near the peak of Sharp Elliot and worked for three or four hours in the forest there. It seemed to be real but rather light rain forest. We found there series of two conspicuous flightless Carabidae: a very big *Nurus* and a *Notonomus*, both endemic. No trace of the four other genera (other than *Notonomus*) discussed above as characteristic of the main tropical and subtropical rain forests of Australia was found. Judging from my experience elsewhere, we would probably have found specimens or fragments of other species if the carabid fauna were diverse. I think, therefore, that the rain forest of the Elliot Range probably has a limited, endemic faunule of flightless Carabidae presumably received across a barrier and not by way of continuous rain forest. The valley that separates the Elliot Range from the main mountain

system of North Queensland is not much more than ten miles wide, but it seems to have been a more effective barrier than the much wider gaps of dry hilly country between the North Queensland, Eungella, and South Queensland rain forest areas.

Summary of Transition from New Guinea to Tasmania

The transition of wet forest carabid faunas from New Guinea to Tasmania involves two main changes. First, between the rain forests of New Guinea and those of tropical Australia is a complete change of flightless stocks of Carabidae and also a change from Agonini to Pterostichini as dominant tribes, although the change is overlain and superficially concealed by many winged species and genera of Carabidae that are common to New Guinea and Australia and that form a broad and complex transition, not fully described here. Between the tropical rain forests of North Queensland and the subtropical ones of South Queensland etc. are very many changes of species and genera but no fundamental change in the nature of faunas or in dominant groups. The second main change is farther south, and is a complex transition from tropical to south temperate groups. The area of transition (of overlapping and mixing of faunal elements) is from the southern edge of Queensland to Tasmania. And the transition involves not only changes of species and genera but a second partial change of dominant tribes, from Pterostichini as principal dominants to (in Tasmania) dominance shared by Broscini and Trechini (and Licinini) as well as some Pterostichini. This change has been described as it occurs among selected flightless geophile Carabidae, but it is reinforced and made more complex by changes of winged Carabidae too.

The whole transition of wet forest carabid faunas from New Guinea to Tasmania might be described as a very irregular stepcline of flightless groups overlain by a more regular transition (or cline of many smaller steps) of winged groups. The flightless Carabidae of the isolated rain forests of Cape York and the Elliot Range are outside the main pattern and complicate it, and of course the situation as a whole is much more complex in detail than I can describe here.

Historical Implications: Two Land Bridges

It is a good working principle of zoogeography that situations should be analyzed first by study of the best known and most significant groups of animals, especially mammals, but that other groups may add important details to what the mammals show. In the present case, two former land bridges are involved: from New Guinea to Australia

and from Australia to Tasmania. Mammals show, by occurrence of many identical or closely related species on opposite sides of the existing water gaps, that both bridges did exist recently and that some forest-living animals crossed both of them. Carabidae show additional, different things about the two bridges. In the case of the Australian-Tasmanian bridge, the Carabidae agree with the mammals. Many wet forest Carabidae including many flightless ones evidently crossed this bridge without meeting important ecological barriers, although cold climate stopped some other animals, especially some reptiles (Darlington 1960, p. 659). In the case of the New Guinea-Australian bridge, however, the flightless rain forest Carabidae show that there was an ecological barrier upon the land, and that the barrier existed for a long time. New Guinea and Australia cannot have been connected by a continuously rain-forested ridge within the time of existing carabid faunas. The recent connection was evidently low and rain forest was probably not continuous across it, although it was nearly enough continuous to allow certain forest trees, mammals, birds, and winged insects to get across. These organisms probably crossed the bridge by way of more or less separate forest "stepping-stones" and strips of gallery forest that did not allow continuous passage of flightless rain forest Carabidae, which do not disperse easily across even narrow gaps of unsuitable land. Rain forest is discontinuous on Cape York now. The Carabidae suggest that it has been so for a long time in the past, and that conditions on Cape York now are like the conditions that existed on the land bridge when New Guinea and Australia were connected.

Historical Implications: Climatic Fluctuations

The present distribution of wet forest Carabidae shows that many of them have been able to move up or down the eastern edge of Australia between North and South Queensland, across what are now wide gaps of comparatively dry country. The degree of relationships of different Carabidae in the tropical and subtropical rain forest systems varies. In some cases (*e. g. Pamborus* of the *tropicus* group) the North and South Queensland representatives of single original stocks are only slightly differentiated, but in other cases (*e. g. Leiradira* and its allies) they have diverged as subgenera or genera. This suggests either several periods of dispersal and isolation, accompanying fluctuations of rainfall and rain forest, or occasional trickling of dominant wet forest Carabidae across the drier gaps of central Queensland. In either case wet forest Carabidae seem to have followed a rather narrow path along the continental divide, and have usually

not been able to reach such slightly isolated places as the rain forest on the Elliot Range. The whole pattern, of occasional or limited exchange between North and South Queensland and of isolation of endemic faunules on the Elliot Range and in the Cape York rain forests, is consistent with climates and forests fluctuating only within moderate limits, not profoundly.

Ecological Correlations

It is a fact not sufficiently understood by some zoogeographers that the climatic zones, the differences between tropical and cool temperate climates, are very important to Carabidae and other insects. In eastern Australia, where climate is the only permanent barrier to dispersal, many old groups of Carabidae are confined to either the tropical (including subtropical) or the cooler south temperate areas. Evidently whole tribes may persist for long periods in small areas protected only by climatic barriers, and even dominant tribes do not always easily cross from one climatic zone to another.

Carabid distribution is correlated with climate and ecology in several more specific ways. For example some rain forest Carabidae, including five genera specially considered above, seem to be more strictly limited to rain forest in the tropics than in the south temperate zone. This suggests that ecological factors are more intense in the tropics, as they may well be if temperature and evaporation rates are involved. That ecological factors are intense in the tropics is suggested also by groups of Carabidae that occur in diverse habitats in the temperate zones but enter or cross the tropics only when associated with surface water, which probably tempers the intensity of tropical climate. I have discussed this elsewhere (1959, especially pp. 332, 342). In Australia, for example, the only Trechini that occur in the tropics are winged hydrophiles: *Perileptus* and *Trechodes* by running water and *Trechobembix* (which extends north to Cairns) in deep swamps. *Mecyclothorax* occurs in many habitats in temperate southern Australia, but I found only one species (apparently *cordicollis* Sl.) in the tropics, in thick vegetation over deep, cool water on the Atherton Tableland. And *Notagonum ("Agonum") submetallicum* (White), which, though always associated with water, occurs in a variety of waterside habitats in both humid and arid parts of south temperate Australia, I found in the tropics (Atherton Tableland) only in thick vegetation over cool, moving water.

There is also a notable correlation of wings and flight of Carabidae with climate and altitude. Carabidae (mostly geophiles) often become flightless at low altitudes in temperate climates, and on moun-

tains everywhere, but rarely at low altitudes in the tropics. The fewness of flightless Carabidae at low altitudes in New Guinea is an example. I have discussed this subject, with other examples, elsewhere (1943).

Finally there is a partial correlation between size of Carabidae and climate. Very large Carabidae (over 1 to 2½ inches long) are numerous in the forests of warm temperate to tropical eastern Australia but relatively few or absent in both cool temperate Tasmania and wholly tropical New Guinea. If *Catadromus tenebrioides* (ol.) is introduced, as I think it is, the largest carabids in New Guinea are hardly an inch long and few are that large. I suspect that this correlation has a complex ecological basis which may include direct action of physiological factors, correlation of size with state of wings and flight, and competition with other insects. Of insects that might compete with carabids, ants are most obvious. I have suggested (1943, p. 42, Fig. 4) that ants may take the place of most flightless geophile Carabidae especially in the lowland tropics.

Geographical History of Carabidae

Carabidae, like other old, complex groups of animals (mammals etc.), have presumably had complex geographical histories, with successive dominant groups evolving, spreading over the world, and replacing older groups. The present distribution of Carabidae in the Australian Region may reflect this. Some localized tribes that are now confined to the cool south temperate zone may be remnants of an ancient fauna (see Darlington 1960 for further discussion of some of these groups). Pterostichini, now dominant in most of Australia, may be more recent and may be replacing more ancient Carabidae. And Agonini may be still more recent, now dominant in New Guinea (and in the whole tropical Asiatic-Australian area), and spreading to Australia.

Pterostichini and Agonini tend, as dominant tribes, to be complementary over the world as a whole. I have discussed this before (1956, pp. 1-3), but what I said then is worth repeating briefly now, with counts of species brought up to date. Both tribes are cosmopolitan, but unevenly so. In some parts of the world they occur in nearly equal numbers, in others, one tribe or the other is overwhelmingly dominant. The tribes tend to be complementary within the Australian Region, as already indicated. In Australia itself (with Tasmania) Pterostichini are dominant, with more than 350 known species against probably less than 20 species of Agonini, a ratio of nearly 40/1. But

in New Guinea Agonini are dominant, with considerably more than 100 known full species (some discovered since my 1952 paper) against about 40 species of Pterostichini (manuscript in press), a *reversed* ratio of about 3/1.

One reason for the number of Agonini in New Guinea is that species of this tribe have multiplied on the mountains there. In Australia, however, Pterostichini, not Agonini, have multiplied in what seem to be comparable habitats on the mountains. This difference can hardly be accounted for in simple ecological terms but is probably due to a complex combination of ecological, historical, and geographical factors. Over the world as a whole, there is a tendency for Agonini to be better represented in the tropics; Pterostichini, in the temperate zones. Also it is probable that Agonini, which are phylogenetically less diverse, are more recent in origin than Pterostichini and that they have dispersed more recently. It is therefore likely that Pterostichini are dominant in Australia partly because Australia is more temperate than tropical in climate and partly because Pterostichini reached Australia before Agonini did, and it is likely that Agonini are dominant in New Guinea partly because the climate there is fully tropical and partly because the carabid fauna of New Guinea is more recent in its origins than that of Australia, as I think it is. Add to this that the mountain carabid faunas of Australia and New Guinea have been derived independently, each from the lowland fauna adjacent to it, and not by dispersal along a connecting mountain chain, and we have an adequate and probably correct explanation of the great difference in composition of the carabid faunas on the mountains of Australia and New Guinea.

As to direction of recent movements of Carabidae, movements of (winged) species have evidently occurred in both directions between Australia and New Guinea, although I cannot take space to give details now. Movements have apparently occurred also in both directions between the tropical and subtropical forests of Australia. This is indicated by the relationship of the species now on the Eungella Range (p. 13), although I am not ready to give further details now. South of the tropics, patterns of distribution (Fig. 7) suggest withdrawal of cool temperate groups and southward spreading of tropical or subtropical groups. This is probably primarily an adjustment to recent warming of climate rather than an invasion of south temperate habitats by tropical Carabidae, although *Pamborus, Trichosternus,* and *Notonomus* have invaded *Nothofagus* forest on high plateaus in New South Wales.

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A RECONSIDERATION OF THE GENUS *EPIPOMPILUS* (HYMENOPTERA: POMPILIDAE)[1]

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The genus *Epipompilus* was described by Kohl in 1884, with *maximiliani* Kohl, from Mexico, as type. It was next treated by Ashmead in 1902, who at the same time described a related genus, *Aulocostethus,* with *bifasciatus* Ashmead, from "Peru", as type, Haupt, in 1930, erected the tribe Epipompilini for these two genera and several others; the others were shortly thereafter removed to another tribe. In 1944 Bradley presented a revision of the American species of *Epipompilus* and *Aulocostethus.* Ashmead, Haupt, and Bradley all separated the two genera by whether or not the eyes are hairy. Since Ashmead said that *Epipompilus* has glabrous eyes, it is clear that he was unfamiliar with the genus; and both Haupt and Bradley admit they had never seen the genus. Thus we have the curious phenomenon of a genus being treated by three persons, none of whom had ever seen any specimens belonging to the genus as he conceived it. As a matter of fact the eyes of *maximiliani* are hairy, and *Epipompilus* as conceived by these three workers is a nonexistent genus: in actuality the name *Epipompilus* is a senior synonym of *Aulocostethus.*

This is only one of several sources of confusion in the genus. Ashmead described *Aulocostethus* by merely placing it in a key and listing *bifasciatus* n. sp. as type. His description of *bifasciatus* can be and has been considered valid, but he gives no information other than the generic characters and the type locality ("Peru"), not even as to color pattern, which is of much value in separating species in this genus. Haupt used Ashmead's name for a specimen from Costa Rica, while Bradley, unable to find Ashmead's type, followed Haupt while expressing doubt that he had correctly identified Ashmead's species. However, there is a specimen in the U. S. National Museum labeled as *Aulocostethus bifasciatus* Ashmead in Ashmead's handwriting and marked as type of that species. But to add to the confusion this specimen bears the locality Bahia, Brazil, not "Peru" as it should. Now Costa Rica (Haupt's specimen) is actually closer to Peru than is Bahia, Brazil, but I find it hard to reason away the identification label in Ashmead's handwriting. Specimens of this genus are so rare that one is unlikely to make an error in labeling; in fact I doubt if Ashmead

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ever saw any other specimens of the genus. On the other hand, Ashmead was a sufficiently careless person so that it is quite believable that he may have jotted down "Peru" when he meant "Brazil". At any rate, I accept this as the type of *bifasciatus* and have presented a description of it below, along with a new name for Haupt's specimen from Costa Rica.

Still further problems remain. Was Ashmead correct in placing *maximiliani* in the synonymy of Cresson's *aztecus,* or was Bradley correct in resurrecting it? If *Epipompilus* and *Aulocostethus* are synonyms, what is the status of Banks' *Epicostethus,* said to share some of the characters of both genera? What is the correct generic placement of *Epipompilus insularis* Kohl, from New Zealand? Finally, what is the male sex of *Epipompilus*?

On the following pages I have presented a brief synopsis of *Epipompilus* in which answers to all of these questions are proposed. I do not mean to imply that all problems in the genus are solved: my synopsis is based on a mere 18 specimens of these exceedingly rare insects. There are doubtless undiscovered species, and the males of most of the species have yet to be found. But at least I hope that I have supplied a sounder framework for future studies than has previously been available.

Genus *Epipompilus* Kohl

Epipompilus Kohl, 1884. Verh. K. K. Zool.-Bot. Gesell. Wien, **34**: 57. [Type species: *Epipompilus maximiliani* Kohl, 1884 (=*aztecus* Cresson 1869) (designated by Ashmead, 1900)].

Aulocostethus Ashmead, 1902, Canad. Ent., **34**: 132. [Type species: *Aulocostethus bifasciatus* Ashmead, 1902 (monobasic and original designation)]. New synonymy.

Epicostethus Banks, 1947, Bull. Mus. Comp. Zool., **99**: 445. [Type species: *Epicostethus williamsi* Banks, 1947 (monobasic)]. New synonymy.

Generic characters. — Maxillary palpi unusually elongate, antepenultimate segment the longest and distinctly longer than third antennal segment; labial palpi with the penultimate segment broadly ovate, the ultimate segment attached to one side of it; mandibles stout, rather smooth, with a few setae but without a lamina on the inferior margin which subtends a fimbriate groove, inner margin with a single strong tooth well back from apex; labrum partially exserted, broad and short, apical margin of clypeus broadly truncate or arcuately concave; flagellum with rather coarse, bristling, semi-erect pubescence, particularly on the inner side of the basal segments of the female and on the outer side of the entire flagellum of the male; head broader than high, front with distinct small punctures; eyes densely covered with short hairs (reduced and scarcely noticeable in some females and in

the known males); front rather swollen above, between the antennal bases abruptly declivous to the much lower plane of the area frontalis and clypeus. Pronotum short or fairly long, sides of disc rather prominent, streptaulus absent or ill-defined; mesoscutellum and metanotum prominent medially, latter with distinct lateral foveae; postnotum of variable length, front and hind margins subparallel; propodeum with smooth contours, slope low and even, almost flat behind; front femora of female slightly to quite noticeably incrassate; front tibiae and tarsi without spines, middle and hind tibiae with or without scattered short spines; segments of front tarsus of female unusually short; claws slender, with a strong, subapical tooth which is nearly parallel to the apical tooth; ultimate tarsal segments without spines beneath, pulvillar pads small but giving rise to some strong setulae. Hind wing with anal lobe small, about .3-.5 as long as submedian cell, anal vein extending very slightly or not at all beyond junction of transverse median vein, latter vein leaving it at an angle, oblique, meeting media much before origin of cubitus; fore wing with venation extending relatively close to outer wing margin, marginal cell acute, removed from wing-tip much less than its own length; three submarginal cells present, second and third receiving recurrent veins near middle, third much wider at apex than at base. Abdomen fusiform, in the female somewhat depressed apically, apical sternite rather flat, even obscurely grooved medially; male with or without conspicuous brushes of hair on sternites four and five, subgenital plate of remarkable structure, forming a very slender, hairy process apically, its basal plate (morphological sternite 8) unusually broad; male genitalia with short, simple parameres, volsellae short-setose, not expanded apically, basal hooklets double, aedoeagus small and of simple structure.

Remarks. — *Epipompilus* possesses a remarkable array of unusual structural features; if one follows the practice of Bradley and Arnold of splitting the Pompilinae into numerous tribes, there can be no question that the genus deserves a tribe of its own. Personally, I am much impressed with certain similarities with *Aporus* and related genera: the pronotum is similar, the front legs of the female somewhat incrassate, and the head shape and hairiness of the eyes suggestive of certain Aporini. The male genitalia suggests *Allaporus*, as does the venation of the hind wing. Any division of the Pompilinae into tribes can be no more than tentative until such time as the classification of the family from a world point of view is more satisfactorily worked out. In the meantime, I prefer to place *Epipompilus* in the Aporini.

As here construed, the genus *Epipompilus* is strictly Neotropical

is distribution. However, Kohl included a New Zealand species, *insularis* Kohl, in his conception of the genus, and various workers since have listed *Epipompilus* from the Australian region. I have studied two females determined by Banks as *insularis* and agreeing well with Kohl's description of this species. There can be no question that this species is closely related to the several Neotropical species of *Epipompilus*. Indeed, it agrees well with the above diagnosis except in the following characters (the males are unknown) : maxillary palpi not greatly lengthened, about as usual in the family; labial palpi unmodified; eyes with only minute, scarcely noticeable hairs; transverse median vein of hind wing reaching media a short distance before origin of cubitus. The generic name *Epipompiloides* is here proposed for *insularis* Kohl, 1884. I know of no other species assignable to this genus, but the pompilid fauna of the Australian region is, of course, very inadequately known. This genus is related to *Epipompilus* and should be placed in the Aporini next to that genus.

Key to known species of the genus *Epipompilus*

Males

Antennae moderately long, crenulate in profile; claws of front tarsus nearly alike; thorax in considerable part rufous; parameres of genitalia with extremely long hairs, abdominal venter with hair-tufts ..... 9. *innubus* n. sp.

Antennae very short, with coarse, dark pubescence but only very weakly crenulate in profile; outer claws of front tarsus much more strongly curved than inner claws; thorax black; parameres and abdominal venter with only short hairs ..... 6. *excelsus* (Bradley)

Females

1. Wings wholly fuliginous; abdomen wholly rufous; pronotum patterned with red and black (Florida and Bahamas) ..... 1. *pulcherrimus* (Evans)

   Wings hyaline, fore wing with two prominent brownish bands; abdomen not wholly rufous, more or less patterned with black, rufous, and/or whitish, pronotum all black or all rufous 2

2. Abdomen black, with a pattern of whitish spots 3

   Abdomen in part rufous, with or without whitish spots 5

3. Body wholly black except for a pair of whitish spots on second abdominal tergite; hind tibiae with a few short spines; pronotum very short, subangulate behind (Ecuador) ..... 2. *williamsi* (Banks)

   Thorax largely rufous; hind tibiae without spines 4

4. Abdomen with whitish markings on tergites 2 and 5, none on sternites; posterior lobes of pronotum rufous (Mexico) .... 3. *aztecus* (Cresson)
   Abdomen with whitish markings on tergites 2, 3, 4, and 5, also on sternites 2 and 3; posterior lobes of pronotum whitish (Brazil) .....4. *bifasciatus* (Ashmead)
5. Size larger (8-11 mm.); abdomen with whitish markings on tergite five, this tergite otherwise black (Brazil) 6
   Size small (6-7 mm.); abdomen not marked with whitish on tergite five, tergites five and six brownish-ferruginous (Central America) 7
6. Antennae black; propodeum black except for limited yellowish markings; hind tibiae unarmed .....5. *haupti* (Arlé)
   Antennae rufous except darker apically; propodeum wholly rufo-castaneous; hind tibiae weakly spinose ....6. *excelsus* (Bradley)
7. Second abdominal segment with a pair of whitish spots; hind tibiae unarmed (Panama) .....7. *delicatus* Turner
   Second abdominal tergite without whitish spots; hind tibiae with scattered, short spines (Costa Rica) .....8. *insolitus* n. name

1. *Epipompilus pulcherrimus* (Evans) new combination

Aulocostethus pulcherrimus Evans, 1955, Ent. News, **66**: 150. [Type: ♀, Everglades Nat. Park, Florida, 30 December 1953 (U. S. Nat. Mus.)].

Remarks. — Since describing this species from the unique type, I have seen one additional specimen, from Mangrove Cay, Andros Island, May-June 1917 (W. M. Mann) [Amer. Mus. Nat. Hist.]. This specimen agrees well with the type except that it is smaller (about 5 mm. long, fore wing 4.3 mm.) and the pronotum has a broad median streak of pale rufous as well as being rufous anteriorly and posteriorly. This species is colored quite differently from any other. The pronotum is much shorter than in *aztecus*, nearly as short as in *williamsi*. The claws are the same as in *aztecus* and other species of the genus, my statement to the contrary in the original description being in error.

2. *Epipompilus williamsi* (Banks) new combination

Epicostethus williamsi Banks, 1947, Bull. Mus. Comp. Zool., **99**: 446. [Type: ♀. Baños, Oriente, Ecuador, 6000 feet, 30 Oct. (Mus. Comp. Zool.)].

Remarks. — Bank's description is detailed and there is no reason to repeat it here. The pronotum is short and subangulate behind, the front femora are barely incrassate, and the hind tibiae have several spines. The first two of these characters are shared (more or less)

with *pulcherrimus* and *delicatus*, the third with *insolitus*, *excelsus*, and *innubus*. Thus the species is not as unique as Banks supposed, and his generic name must be added to the synonymy of *Epipompilus*. I have seen no specimens of this species other than Banks' type.

3. *Epipompilus aztecus* (Cresson) new combination

Ferreola azteca Cresson, 1869, Proc. Boston Soc. Nat. Hist., 12: 376 [Type: ♀, Veracruz, Mexico (Acad. Nat. Sci. Phila.)].
Epipompilus maximillian. Bradley, 1944, Trans. Amer. Ent. Soc., 70: 146
34: 57 [Type: ♀, Cuernavaca, Mexico, 1871 (Bilimek) (Vienna Mus.)]. (Placed in synonymy with *azteca* by Ashmead, 1902). — Haupt, 1930. Mitt. Zool. Mus. Berlin, 16: 762.
Epipompilus maximilliani Bradley, 1944, Trans. Amer. Ent. Soc., 70: 146 (Misspelling of *maximiliani* Kohl).
Aulocostethus aztecus Bradley, 1944, ibid., p. 142.

Remarks. — Bradley has recently provided a detailed description of this species, drawn from Cresson's type of *azteca*. He states that this specimen "does not at all agree with Kohl's description of *maximiliani*". Since I found myself unable to agree with this statement, I asked to borrow the type of *maximiliani* from the Vienna Museum for comparison. At first the type could not be located, but later Dr. R. M. Bohart visited the museum and at my request searched for and found it; Dr. Max Fischer then sent it to me by mail, and I took it to Philadelphia and compared it directly with the type of *azteca*. I am very much indebted to Drs. Bohart and Fischer for their assistance with this problem.

The two type specimens differ considerably in size, that of *aztecus* being much larger, 13.5 mm. long, fore wing 10 mm.; *maximiliani* measures 7.5 mm. long, fore wing 6 mm. The front femora are slightly more incrassate in *aztecus* (2.6 × as long as maximum width as compared to 2.75 × in *maximiliani*). The whitish maculations are exactly the same in the two specimens, but they type of *aztecus* has the posterior third of the propodeum blackish and the middle and hind legs blackish except for the white spurs and white streaks on the hind tibiae; in the type of *maximiliani* the propodeum is wholly rufous, the middle and hind coxae rufous above, the middle and hind femora rufous, and the tibiae partially suffused with rufous. Besides these two specimens, I have seen one other, a female from Cuernavaca, taken by my wife inside the window of a house on March 24, 1959. This specimen is about the same size as the type of *aztecus*, from Veracruz, and the front femora are incrassate to the same degree. However, the propodeum is wholly rufous (as in the type of *maximiliani*, also from Cuernavaca) and the leg coloration intermediate between that of the two types (middle femora rufous, hind femora

black, middle tibiae slightly suffused with rufous but hind tibiae black and whitish, middle and hind coxae with a small amount of rufous above). There is no question at all in my mind that these three specimens are conspecific.

4. *Epipompilus bifasciatus* (Ashmead) new combination

Aulocostethus bifasciatus Ashmead, 1902, Canad. Ent., 34: 132 [Type: ♀, Bahia, Brazil, 19 March 1883 (but stated by Ashmead to be "Peru") (U. S. Nat. Mus., no. 58858)]. (Not *Aulocostethus bifasciatus* of Haupt, 1930; see no. 8, *insolitus* n. name).

Description of type female. — Length 11 mm., fore wing 8.7 mm. Head black; inner orbits narrowly pale yellow up to emargination of eyes; antennae wholly brownish, darker apically; apical half of clypeus and labrum pale yellowish; mandibles dull rufous; palpi light reddish-brown. Thorax rufo-castaneous, except mesonotum with black streaks over wing bases, and the following pale yellow: posterior lobes of pronotum, extreme lower posterior corner of mesopleurum, posterior rim of propodeum (interrupted medially), and apical posterior parts of middle and hind coxae; legs otherwise reddish like thorax, middle and hind tibiae weakly infuscated, spurs all whitish. Abdomen black, spotted with pale yellow (almost white) as follows: two large lateral spots on tergite two, two much smaller spots on tergite three, two spots on tergite four slightly larger than those on three, two large spots on tergite five broadly connected by a basal band; also sternites two and three with small lateral spots. Wings bifasciate, hyaline with a strong band over the basal and transverse median veins and a broader band filling the marginal cell and extending to the posterior wing margin. Body and legs clothed with short, white hair; eyes short-haired.

Clypeus broadly truncate; labrum small, exserted. First four antennal segments in a ratio of about 13:5:11:12, segment three .55 × upper interocular line. Head 1.2 × as broad as high; middle interocular line .57 × width of head; upper interocular line .8 × lower interocular line. Ocelli in a broad, flat triangle, front angle greater than a right angle; postocellar line much greater than ocello-ocular line. Pronotum of moderate length, posterior margin subangulate. Propodeum with smooth contours except posterior slope finely transversely striolate and with rather long pubescence; median line not impressed. Posterior tibiae without spines. Fore wing with basal and transverse median veins interstitial; radial vein somewhat angulate at junction of second intercubital vein, marginal cell removed from wingtip by about .7 its own length.

Remarks. — This is a rather typical member of the genus, in fact

rather close to *aztecus*. As mentioned in the introduction, Ashmead provided no real description of the species, and Bradley did not see the type and therefore followed Haupt, who had misidentified the species. Presumably Ashmead was merely in error when he gave "Peru" as the type locality of the species, as the type is labeled in Ashmead's handwriting.

5. *Epipompilus haupti* (Arlé) new combination

Aulocostethus haupti Arlé, 1936, Festschr. für Embrik Strand, 1: 514 [Type: ♀, Serra do Realengo, Rio de Janeiro, Brazil, 7 Oct. 1934].—Bradley, 1944, Trans. Amer. Ent. Soc., 70: 144. —Banks, 1947, Bull. Mus. Comp. Zool., 99: 445.

Remarks. — Bradley has provided a translation of the description of this species. I have studied the specimen mentioned by Banks (Campinas, Brazil). The legs of this specimen are more extensively rufous than described for the type, but there is agreement in most other details; the eyes of this species are more weakly hairy than is usual in the genus.

6. *Epipompilus excelsus* (Bradley) new combination

Figs. 3 and 4

Aulocostethus excelsus Bradley, 1944, Trans. Amer. Ent. Soc., 70: 143 [Type: ♀, Nova Teutonia, Santa Catarina, Brazil, 25 January 1939 (Mus. Comp. Zool.)]. —Wahis, 1957, Bull, Ann. Soc. R. Ent. Belg., 93: 47-49 (Remarks on color variation).

Remarks. — I have seen several additional females of this species from the type locality, as well as a female from Rio de Janeiro, October 1938 (R. C. Shannon) [U. S. Nat. Mus.]. The type, as well as all the other specimens I have seen, has a pair of connected whitish spots on the fifth tergite, Bradley's description being in error on this point. Wahis has discussed this matter and also pointed out that some specimens have whitish markings on the second and sixth tergites.

A male *Epipompilus* in the Canadian National Collections, Ottawa, is almost certainly that of *excelsus*, even though it is colored very differently from the female. Like the type female *excelsus*, it was taken at Nova Teutonia, Brazil, by Fritz Plaumann, in this case on 19 June 1946. The spinose hind tibiae, as well as the locality, suggest that this male belongs here rather than with *haupti* or *bifasciatus*.

Description of male. — Length 5.8 mm., fore wing 4.8 mm. Body wholly shining black, with a weak bluish luster; face with a pair of small whitish spots beside and below the antennal sockets, next to the eyes; apical two thirds of mandibles whitish, the teeth rufous; palpi

light brown; antennae dark brown; tegulae dark brown; front and middle legs with the coxae black, suffused with brown apically, remainder of these legs brown, middle femora with a tinge of rufous, front tibiae yellowish-brown; hind legs wholly black except tibia with a sub-basal whitish spot which nearly encircles them; fore wing weakly tinged with brownish, especially along the basal vein and on the apical third, setulae dark, veins and stigma brown.

Maxillary palpi with segments 3-6 in a ratio of about 15:19:15:13. Mandibles with a single large tooth well back from apex. Clypeus arcuately emarginate apically, exposing the small labrum. Eyes strongly convergent below, lower interocular line about .75 × upper interocular line; middle interocular line. .59 × width of head; head about 1.15 × as wide as high; ocelli in a broad triangle, postocellar line 1.3 × ocello-ocular line. Front with distinct punctures which are separated by about their own diameters. Eyes with minute hairs except near the tops, where they are somewhat longer. First four antennal segments in a ratio of about 15:5:8:9, segment three about 1.6 × as long as thick; flagellum short, very weakly crenulate in profile, with coarse, dark pubescence which is especially long and suberect on the upper and outer sides of the basal segments.

Pronotum of moderate length, its posterior margin subangulate. Mesonotum wholly and uniformly covered with small punctures. Postnotum nearly as long as metanotum, polished, with a median impression and some weak basal striations. Propodeum with the slope low and even; median line not impressed. Femora slender; middle tibiae with a few spines, hind tibiae with many fairly strong spines above; all tarsi weakly spinose; longer spur of hind tibiae nearly as long as basitarsus. Claws with the inner tooth of all claws strong, sloping so that the claws appear bifid; outer claws of front tarsus much more strongly curved than inner claws. Fore wing with basal vein arising a very short distance beyond transverse median vein, basal part of basal vein distinctly arched; marginal cell large, acute apically, radial vein distinctly angulate at its junction with the second transverse cubital vein.

Abdomen fusiform, covered with short setae but without distinct ventral hair-brushes. Subgenital plate (fig. 3) consisting of a long, hairy apical process arising from a basal section which also bears some long hairs. Genitalia (fig. 4) with the parameres weakly setose; volsellae simple, weakly setose; basal hooklets large, double; parapenial lobes somewhat knobbed apically, very slightly exceeding the volsellae.

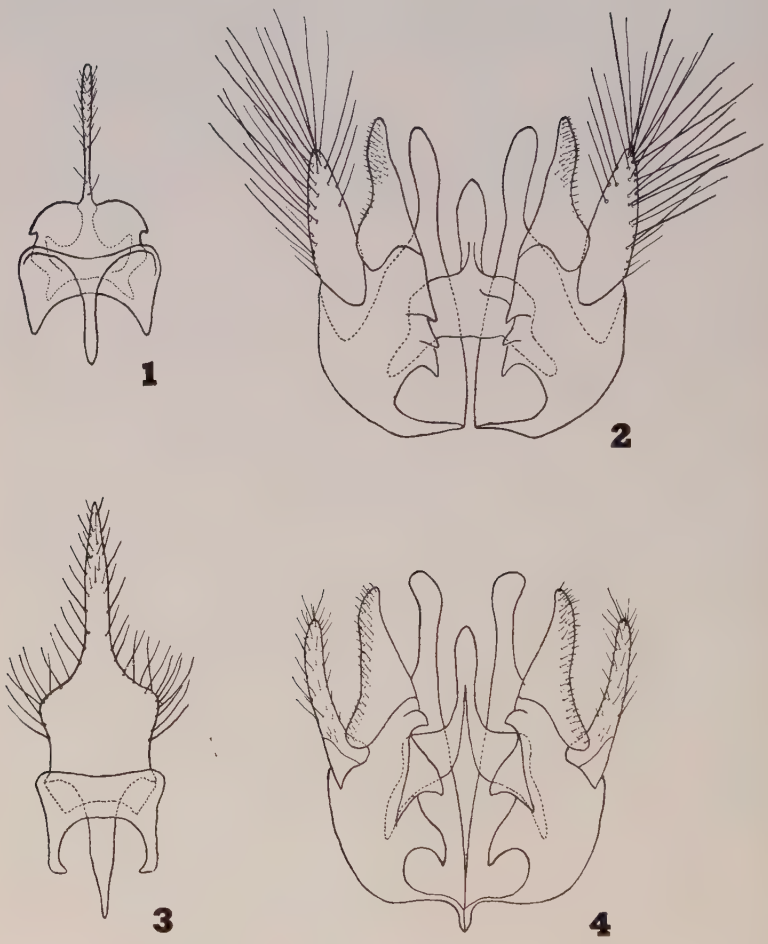

FIG. 1 Subgenital plate of *Epipompilus innubus* new species. FIG. 2 Genitalia of *E. innubus*. FIG. 3 Subgenital plate of *E. excelsus* (Bradley). FIG. 4 Genitalia of *E. excelsus*. All figures show the ventral aspect.

7. *Epipompilus delicatus* Turner

Epipompilus delicatus Turner, 1917. Ann. Mag. Nat. Hist., (8) 20: 359 [Type: ♀, Bugaba, Panama (Champion) (British Mus.)].—Bradley, 1944, Trans. Amer. Ent. Soc., 70: 146.

Remarks. — I have not seen the type of this species, nor had Bradley. It is a small species, comparable in size to *pulcherrimus* and *insolitus*. It is reported to have a short pronotum and unarmed hind tibiae, as well as a color pattern distinct from that of other species.

8. *Epipompilus insolitus* new name

Aulocostethus bifasciatus Haupt, 1930. Mitt. Zool. Mus. Berlin, 16: 763. — Bradley, 1944, Trans. Amer. Ent. Soc., 70: 145 (*Nec* Ashmead, 1902, Canad. Ent., 34: 132; misidentification).

Type. — ♀, Turrialba, Costa Rica (Coll. H. Haupt, Halle/Saale, Germany).

Description (from Haupt, 1930). — Length 7 mm. Yellowish-brown, the following black: head, apical half of antennae, tergites 1, 3, and 4, apex of hind femora, and outer base of hind tibia. Fore wing with two dark brown bands. Hind tibiae with a whitish area behind the black base, tips of front and hind coxae also whitish. Whole body with short, thick whitish hair; eyes and wings hairy.

Wings (Haupt's fig. 64) yellowish-hyaline, a brown transverse band before the middle and one before the apex. Fore wing with three cubital cells, the second somewhat pentagonal, the third trapezoidal, the latter removed from tip by its own length. Radial cell longer than second and third cubital cells together, also somewhat higher than these. Pterostigma cell-like, translucent, somewhat attenuate. Lower section of basal vein about twice as long as upper and weakly arched; transverse median vein interstitial. Hind wing with transverse median vein short, oblique, reaching media more than its own length before origin of cubitus.

Head thick, flattened and weakly concave immediately behind the eyes, temples barely developed. Ocelli large, forming a weakly acute angle in front, postocellar and ocello-ocular lines equal. Front strongly swollen, eyes thick, their inner margins subparallel, the eyes together about equal to width of front. Antennae filiform, relatively thick, third segment somewhat shorter than scape. Clypeus short, trapezoidal, its entire anterior margin weakly arcuately concave. Segments of maxillary palpi very long, third segment about ten times as long as thick (Haupt's fig. 65). Pronotum short, hind margin obtusely angled, sides parallel, with distinct longitudinal swellings. Mesoscutum twice as long as pronotum medially; scutellum and metanotum

elevated. Postnotum distinct, half as long as metanotum, lightly impressed medially. Propodeum somewhat longer than broad, narrowed and less steeply sloping behind, without discernible sculpturing except indication of a median groove. Fore tarsi without a comb, second to fourth segments short, the second as long as broad, the following shorter. Hind tibiae with scattered, short spines. Claws slender, with a sharp tooth before the apex, also with a distinct fan of bristles (Haupt's fig. 84J); claw-comb with a very short plate, its barbules sparse, surpassing the pulvillus.

Remarks. — I have not seen this species, but since it has been described and figured by Haupt in considerable detail, it seems desirable to provide a name for it.

9. **Epipompilus innubus** new species
Figs. 1 and 2

Type. — ♂, Cucharas, 750 m., Valley of Huallaga, Dpt. Huanuco, Peru, June 1954 (F. Woytkowski) [Coll. H. K. Townes].

Description. — Length 6 mm., fore wing 5.7 mm. Head black except as follows: inner orbits pale yellow up to middle of eyes; clypeus, labrum, and mandibles pale yellow, almost white; palpi very light brown; antennal sockets connected by a light yellow band; first five antennal segments yellowish-brown below, dark brown above, rest of antenna nearly black. Thorax rufo-ferruginous except shining blue-black as follows: propleura and extreme anterior parts of pronotum, mesosternum and anterior half of mesopleurum, sides of metanotum, all of postnotum, all of metapleurum except upper anterior margin, all of propodeum except for sides of posterior rim, which are pale yellow. Coxae blackish except middle and hind coxae tipped with white; middle and hind trochanters blackish; front and middle legs otherwise light reddish-brown, hind legs nearly black except tarsi paler and tibiae with a white basal annulus; tibial spurs whitish except middle and hind spurs suffused with black basally. Abdomen shining blue-black except apical tergite ivory-white. Wings hyaline, with dark setulae, veins and stigma brown, fore wing weakly clouded in and about third submarginal cell.

Maxillary palpi very long, segments in a ratio of about 2:4:8:10:8:7. Mandibles rather smooth, with a few setae, inner margin with a strong tooth well back from apex. Labrum broad and short, truncate, exserted well beyond truncate apical margin of clypeus, latter about twice as broad as high. Front prominent above antennal orbits, narrow, middle interocular line .56 times width of head; head nearly 1.2 × as wide as high; ocelli in a broad, flat tri-

angle, postocellar line twice the ocello-ocular line. Front with distinct punctures which are separated by less than their own diameters. Eyes with very short, barely noticeable hairs. First four antennal segments in a ratio of about 15:5:13:12, segment three about twice as long as thick; each flagellar segment, but more particularly the middle ones, with a distinct swelling below and toward the base, giving the antennae a somewhat crenulate profile below.

Pronotum very short, its posterior margin subangulate. Mesonotum with distinct small punctures like the front; postnotum smooth, transversely striate, about half as long as metanotum. Propodeum with even contours, median line weakly impressed, surface of declivity very finely transversely striolate. Femora not notably swollen; middle and hind tibiae with short spines scattered amongst the pubescence; longer spur of hind tibia nearly as long as basitarsus; claws of front and middle legs strongly dentate, those of hind legs obscurely dentate. Fore wing with basal vein arising well beyond junction of transverse median vein, basal part of basal vein strongly arched; marginal cell large, acute, removed from wing-tip by only about half its length; other features of wing about as in other species of the genus.

Abdomen fusiform, covered with short setae; sternites four and five each with a transverse brush of longer setae, longer on the sides than medially, the setae curved at their tips; genitalia also giving rise to some long setae which protrude from sides of subgenital plate. Subgenital plate (fig. 1) of unusual form, consisting of a long, slender, hairy process arising from complex basal plates (the modified ultimate and penultimate sternites). Genitalia (fig. 2) with parameres short, bearing some very strong setae; volsellae weakly setose, narrow in ventral view but mesal surface wide and concave; basal hooklets double, unusually well separated; parapenial lobes slightly shorter than volsellae; aedoeagus very small.

Remarks. —The spinose hind tibiae and short pronotum suggest *williamsi* as the possible female of this species, and the type localities of these two are not too far distant (Ecuador and Central Peru). However, the difference in coloration is great, and it seems to me best to consider the two distinct for the present.

THE REDISCOVERY AND PROBABLE PHYLOGENETIC POSITION OF *PSILOPSOCUS* (PSOCOPTERA)

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The genus *Psilopsocus* has posed a puzzle to students of the Psocoptera since the time of its discovery. The original description by Enderlein (1903: 305) was based on a single specimen. Although adequate for identification, this description does not permit the genus to be placed beyond suborder in recent classifications. Enderlein placed *Psilopsocus* in the Mesopsocidae, but gave no reasons for this. Roesler (1944), apparently without re-examining the type, erected a new family for this genus and placed it in the group Epipsocetae on the basis of similarity of the lacinia in the Epipsocidae and Psilopsocidae.

It is the purpose of this paper to describe a new species of *Psilopsocus* from the Philippine Islands, to add to the knowledge of the morphology of the genus, and to re-interpret its phylogenetic position.

Genus *Psilopsocus* Enderlein, 1903.

In addition to the characters included by Enderlein in the original description, the following characters are probably important in delimiting this genus:

1. Male phallic sclerotizations in the form of a simple frame with no indication of external parameres (fig. 2.).
2. Ovipositor valvulae complete, i.e. three pairs.
3. Female subgenital plate with a slender central process (fig. 1.).
4. Female paraproct with a decided elongation of the posterior margin (fig. 3.).
5. Male paraproct with a pointed apical process on its posterior margin (fig. 8.).
6. Labrum not of the *Epipsocus* type, lacking a pair of diagonal strap-like sclerites.

The character mentioned by Enderlein of lack of junction of the

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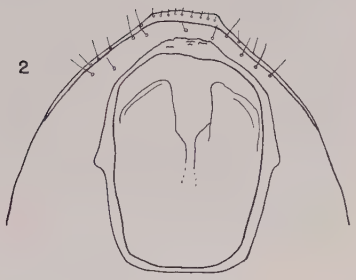
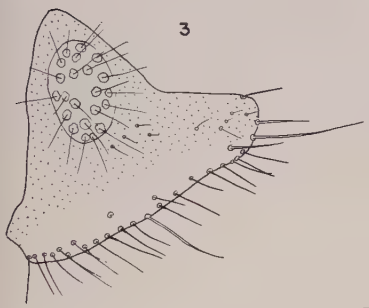
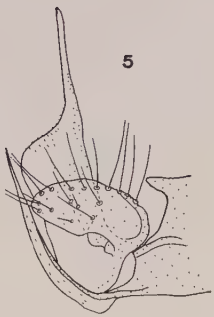
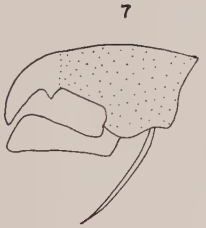
Explanation of Plate 5

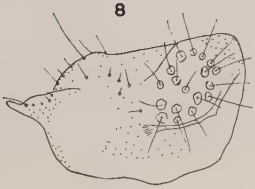
Psilopsocus nebulosus n. sp. Fig. 1, ♀, subgenital plate. Fig.2, ♂, hypandrium and phallic frame. Fig. 3, ♀, left paraproct. Fig. 4, ♀, sclerites of 9th abdominal sternite (dorsal view). Fig. 5, ♀, ovipositor valvulae. Fig. 6, ♂, lacinial tip. Fig. 7, ♂, tarsal claw. Fig. 8, ♂, right paraproct. Fig. 9, ♂, tip of pedicel (Ped.) and base of first flagellar segment (fl).











MOCKFORD — PSILOPSOCUS

bases of Radius and Media + Cubitus in the hindwing is not found in the species described below, although a fold in the wing membrane running from the Radius just above this junction, to the wing base produces the appearance of two closely parallel veins.

In the species described below, the coxal organ is well developed, with both rasp and tympanum. The rasp is composed of tiny indentations with raised edges.

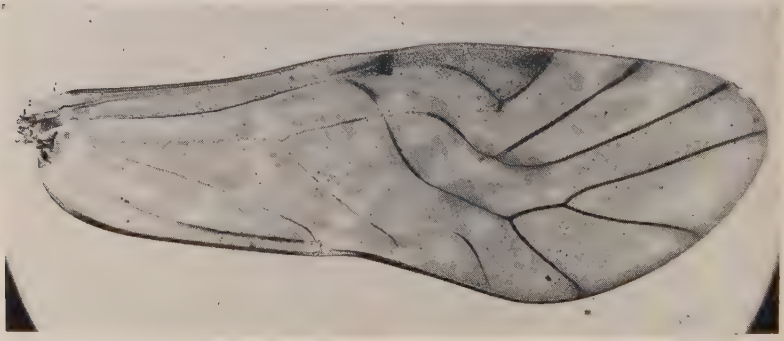
Psilopsocus nebulosus, new species

Plate 5 and Text Fig. 1

Diagnosis: differs from the generotype, *P. nigricornis* End., possibly in number of teeth on lacinial tip (6 indicated for *nigricornis,* 11 in *nebulosus*), number of ctenidia on basal segment of hind tarsus (15 in *nigricornis,* 16 to 19 in *nebulosus*), shape of the pterostigma (less deep in *nebulosus*), and details of the forewing markings (text figure 1), colorless areas being more numerous in *nebulosus,* but there being no colorless areas bordering the wing apex in this species.

Holotype ♂. Measurements (see table I.).

Morphology: IO/D (distance between eyes divided by greatest dorsal diameter of eye, method of Badonnel) = 0.78, PO (lateral diameter of eye from above divided by greatest dorsal diameter of eye) = 0.94. Apex of lacinia (fig. 6.) broad, with a distinct lateral and median cusp, the lateral broadest and bearing 10 denticles. Coeloconic sensilla of first flagellar segment two in number, both situated at the extreme base of the segment (fig. 9.). Distinct tarsal ctenidia present only on posterior tarsi, with a row of 17 on T1 and one each on T2 and T3 (T1 = basal tarsal segment). Hypandrium weakly sclerotized, its margin rounded except slightly flattened at the apex; this flattened apex slightly more heavily sclerotized than



Text figure 1. *Psilopsocus nebulosus* n. sp., ♂, photomicrograph of right forewing.

the rest of the hypandrium and bearing a row of tiny cilia (fig. 2.). Phallic frame (fig. 2.) a simple ring, slightly oblong, rather uniform in width except somewhat thickened apically and for a short distance along each side. Within the frame are a pair of membranous lobes. Paraproct (fig. 8.) with the usual field of trichobothria extending obliquely downward from its antero-dorsal angle. Posterior margin of the paraproct extended as a lobe tipped with a pointed process.

Color (in alcohol): compound eyes black. General body color dull ivory marked with medium to pale brown. Labrum, antennae, ocellar interval, and terminal two segments of maxillary palpi medium brown. Clypeal striations, cloudy spots around compound eyes and antennal bases, and a band bordering epicranial suture pale brown. Thorax irregularly mottled with large pale brown areas including most of the pleura and large areas of the tergal lobes. Brown areas of mesothoracic tergal lobes darkest at their borders, pale in their centers. Legs dull ivory except medium brown on each coxa, distal end of each femur, distal end of each tibia, and all of each tarsus. Forewing hyaline, marked with extensive pale brown cloudy bands and spots as in text figure 1. Abdomen ringed with irregular pale brown cloudy bands. Terminal segments medium brown.

Allotype ♀. Measurements (see table I).

Morphology: IO/D = 1.56, PO = 0.72. Tarsal ctenidia present only on posterior tarsi with a row of 18 on T1 and one each on T2 and T3. Subgenital plate (fig. 1.) with basal pigmented area in the form of two widely diverging arms. Median process of subgenital plate broad basally, abruptly narrowing to a slender tongue about half-way toward its tip; the broad basal portion bearing two large setae and the slender apical portion bearing many setae of various sizes. Sclerites of the 9th abdominal sternite (fig. 4.) in the form

Table I. Length (in mm.) of various characters of *Psilopsocus nebulosus*

Character	♂	♂	♂	♂	♀
Entire body	2.87	2.82	2.61	3.03	3.67
Forewing	4.44	4.40	4.44	4.59	4.65
Hind tibia	1.39	1.43	1.43	1.57	1.43
Hind tarsus, T1*	0.465	0.440	0.476	0.476	0.405
Hind tarsus, T2	0.071	0.071	0.059	0.071	0.059
Hind tarsus, T3	0.119	0.119	0.131	0.131	0.119

* First posterior tarsal segment.

of a transverse ring with three straps radiating from it and a transverse strap basal to it. Ovipositor valvulae (fig. 5.) with first valvula slender; second valvula broad basally, terminating in a long, slender process; third valvula a broad flap bearing many setae. Paraproct (fig. 3.) with field of trichobothria in its antero-dorsal angle. Posterior margin of paraproct markedly protruding; ventral and posterior margins bearing many setae.

Variation: aside from variations noted in the descriptions and measurements (table I), four male paratypes have wing and body markings somewhat paler than the holotype male, but this may be due to tenerality. IO/D ratios for three male paratypes are 0.69, 0.70, and 0.70; PO ratios for these are 0.88, 0.85, and 0.91; numbers of ctenidia on posterior basal tarsal segment are 16, 19, and 18.

Nymph: one nymph taken with adults of *P. nebulosus* is with little doubt this species. The association is made on the basis of similarity in size, color, (except the distal two-thirds of the abdomen is dark brown in the nymph), and general body shape, also on the structure of the lacinia and tarsal claws. The lacinia is broad apically with several indistinct denticles on the outer cusp. The tarsal claw bears a preapical tooth and a pulvillus of medium width bent at a decided angle near its base, as in the adult (fig. 7.).

Type locality: Philippine Islands: Mindanao, east slope of Mt. McKinley, Davao Province, August and September, 1946, in mossy forest, elevation 6400 feet, H. Hoogstraal collector; holotype ♂, allotype ♀, 4 ♂ paratypes and one nymph, all in collection of Chicago Natural History Museum.

Discussion: *Psilopsocus* is apparently very close to the Myopsocidae. The following points of similarity were noted:

1. Tarsal structure
   a. Number of segments same.
   b. Distribution of ctenidia same.
   c. Both with preapical tooth on tarsal claw.
   d. Pulvillus in both of medium width with a decided bend near its point of attachment.

2. Lacinial structure. The lacinial tip of *Lichenomima sparsa* has a broad lateral cusp bearing 13 stubby denticles, and a short median cusp, hence it shows marked similarity to the lacinial tip of *Psilopsocus*.

3. Male genitalia.

   a. Hypandrial margin. The rounded hypandrial margin of *Psilopsocus* is similar to that of several species of *Rhaptoneura, Phlotodes,* and *Lichenomima.*

b. Phallic frame. The simple, rounded phallic frame of *Psilopsocus* bearing a pair of lateral thickenings and enclosing a pair of membranous lobes is reminiscent of this structure in *Lichenomima pauliani* Bad. (Badonnel, 1955, fig. 529) and *Rhaptoneura eatoni* McL. (Badonnel, 1943, fig. 143). It differs little from this structure in *Lichenomima maxima* Sm. (Smithers, 1957, fig. 6).

c. Paraproct. The paraproct of *Psilopsocus* is similar to those of most Myopsocids in bearing a pointed process on its posterior margin. Although several species of Myopsocids have two such processes, there is only one in *Phlotodes angolensis* Bad. (Badonnel, 1955, fig. 514). The male paraproct of the latter species resembles that of *Psilopsocus* in several other respects, including shape of the field of trichobothria and presence of a roughened area antero-dorsad of this field.

4. Female genitalia.

a. Subgenital plate. The subgenital plate of *Psilopsocus* is similar in structure to that of *Rhaptoneura*. The resemblance is especially marked in the case of *R. africana* Bad. (Badonnel, 1955, fig. 508). In both forms the pigmented basal area consists of a pair of widely diverging arms; the central process is broad basally, narrowing abruptly to a slender tongue which bears setae on or near its apex.

b. Ovipositor valvulae. Both *Psilopsocus* and the Myopsocids have three pairs of ovipositor valvulae. The second valvula terminates as a long, slender process in both groups, although this is generally much longer in the Myopsocidae than in *Psilopsocus*. The third valvula is a simple flap bearing many setae in both groups.

c. Sclerites of the ninth abdominal sternite. These sclerites in several *Lichenomina* species (Badonnel, 1955, figs. 522-525; Smithers, 1957, fig. 11) are composed of three main sclerotized areas, and are thus similar in appearance to the same group of sclerites in *Psilopsocus nebulosus* with their three radiating sclerotized straps.

d. Paraproct. The female paraproct is similar in shape, ciliation, and position of the field of trichobothria in the two groups.

The differences between the Myopsocidae and the Psilopsocidae are not great. The only ones which I have found are (1) presence in Myopsocidae of a connection between areola postica and medial stem in the forewing and absence of this in Psilopsocidae, (2) presence in Psilopsocidae of a spur vein from the pterostigma and its absence in Myopsocidae, and (3) much more complex markings of the forewing in Myopsocidae than in Psilopsocidae, with characteristic alternating dark and light areas on veins in the former group.

Pearman (1936) has designated the families Myopsocidae, Psocidae, and Thyrsophoridae as constituting the group Psocetae. To this group should be added the Psilopsocidae. It appears that this group represents an ancient phylogenetic line within the suborder Psocomorpha, in which the most primitive forms share a broad, multidenticulate lacinial tip with the Group Epipsocetae. It seems likely that this type of lacinial tip, found also in the Amphientomidae (Suborder Troctomorpha) was present in the earliest forms of the Suborder Psocomorpha.

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